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VISUAL MATING SIGNALS. Evolution has sculpted and colored the surfaces of the arthropod body. Natural selection favored appearances that mislead predators through disguise and camouflage, i.e., 'cryptic coloration,' and those that warn enemies to stay away through bright advertisements of distastefulness or dangerous weapons, i.e., 'aposematic coloration.' In addition, body surfaces may help modify the effects of the physical environment, e.g., to absorb or reflect heat. Certain colors, shapes and movements also influence the behavior of the conspecifics in contexts including social interactions, e.g., honeybee dances. Other signals evolved in the context of mating.

Sexual selection and the evolution of displays

These sex-related signals, or 'displays,' are directed either toward rivals (usually males attempting to repel other males) or potential sexual partners (usually males attempting to attract mate-choosing females). Display surfaces, and the behaviors associated with their exhibition, have evolved through sexual selection, the process in which genes are ancestral coloration for one that offered more protection from predators.

However, not all sexual dimorphisms in color are the direct result of sexual selection. For example, male and female stick insects (Phasmatodea), such as *Diapheromera covilleae*, sometimes bear special resemblance to different types of foliage on their host plants, and while the two sexes look quite dissimilar, there is little in their mating behavior to suggest a visual display is the cause of the difference. On the other hand, surfaces and colors that are not sexually dimorphic may be used in displays. Movements of strikingly patterned wings are typical of sexual encounters in fruit flies (Tephritidae), but sexual dimorphism in wing coloration and marking is rare.

The advantages and disadvantages of light in communications

In comparison to chemicals and sounds, reflected light perceived as color and pattern has both advantages and disadvantages as a means of communication in insects. Among its advantages are its capacity to carry large amounts of reliable information. A signal is able to transmit a message through modulation, predictable and specific variations, e.g., Morse code, or a particular color pattern on the surface of a wing. Visual cues may be more reliable in this sense than chemicals whose combinations and densities can be blended and obscured by even slight motions of the air. It is difficult to imagine a message consisting of patterned puffs of odor making sense to a distant receiver on a breezy day.

Some modes of communication work better than others in a given habitat and context. Among the potential disadvantages of visual displays are that they can be blocked by opaque objects that chemicals or sounds could go around, and are unlikely to reach as far as pheromones and acoustic signals. Visual signals also lack persistence in the absence of the signaler, e.g., ant recruitment trails. They can even be dangerous to the signaler, as they may be more easily tracked by predators than pheromones or sounds, and even provide an unusual opportunity for predators to lure mate-seekers. For example, fireflies (Lampyridae) can be tricked by 'aggressive mimics' that produce the luminous sexual display-response that attracts males of other firefly species to their final rendezvous.

Arthropod visual signals are potentially detailed and informative, but only at short distances. The effective range of visual signals is generally limited because only a small body-surface area is available for a display and because of the poor resolution of the insect compound eye. Insect eyes can resolve details of little objects such as other insects, but only at extremely close range (''[compound eyes]...would give a picture about as good as if executed in rather coarse wool-work and viewed at a distance of a foot'' [Henry Mallock]). One possible exception to the generally short range of arthropod visual signals is bioluminescence, e.g., the flashes of fireflies. An extreme example is the mass display of male *Pteroptyx* fireflies, which gather by the thousands in certain trees and flash synchronously.

Idiosyncratic details of a particular arthropod's vision also influence the forms of its visual displays. For example, jumping spiders (Salticidae) see colors and are able to detect motion while moving, but wolf spiders (Lycosidae) are color-blind and must be still to perceive movement. Jumping spiders use bright colors and 'dances' in their displays, while wolf spider courtships consist largely of raising and waving darkly pigmented or hairy legs.

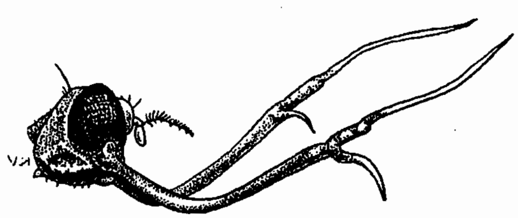

Fig. 1121 The head of a male antlered fruit fly (*Phytalmia cervicornis*) from New Guinea. The deer-like antlers projecting from the cheeks are as much visual propaganda as weapons (drawing by Kevina Vulinec from Sivinski 1997).

UV markings

Human and arthropod vision differ in the range of light wavelengths perceived. Insects are generally insensitive to red, but can see ultraviolet light (UV). Insects that appear drab to us may, in fact, be brightly reflective in the ultraviolet range and able to communicate among themselves in color patterns that are invisible to us and perhaps invisible to some of their vertebrate predators (although diurnal birds typically see UV, as do some mammals). For example, males of certain butterflies (e.g., *Colias* spp. [Pieridae]) bear brilliant UV markings, but the extensive sexual dimorphism in these species was only discovered through specialized photography. As a result, use caution in interpreting a particular arthropod's colors until the entire spectrum is described.

The content of intrasexual displays

As Charles Darwin noted, "The season of love is that of battle...," and conflicts among sexual competitors, usually males, are sometimes resolved by threats communicated through visual displays. The intensity of aggression ('agonistic behaviors'), and the investment in the colors, structures and behaviors that convey the sender's ability to fight, follows a pattern. The greater the control a male can exercise over females or the resources females require, such as oviposition or feeding sites, the more profitable it is for males to invest in weapons and advertisements of prowess. Typically, controllable resources are relatively small and rare and, thus, easily defended. As resources become common, large and spread out, they become less and less defendable and less and less likely to be associated with aggressive displays.

Antlered flies (Diptera) are classic examples of displaying males guarding a discrete resource. Projections from the head, either eye-stalks or horns sprouting from the cheeks, occur in species from nine families of flies. Perhaps the most elaborate are found in the large New Guinean fruit flies (Tephritidae) of the genus *Phytalmia*, one species of which the great 19th century naturalist Alfred Wallace described in the following manner: "The horns of (*P. megalotis*) are about one third the length of the insect, broad, flat, and of an elongated triangular form. They are of a beautiful pink color, edged with black, and with a pale central stripe. The front of the head is also pink, and the eyes violet pink, with a green stripe across them, giving the insect a very elegant and singular appearance."

Female *Phytalmia* oviposit in pinhole sized punctures in certain species of freshly fallen trees. These very small and rare resources attract females and are easily defended, and the owner's initial defense is accomplished through visual display. Resident (defending) and intruder males of *P. mouldsi* clash by rising up on their legs and pushing hard against each other's remarkable heads, although the antlers themselves do not play a major role in the battle. However, males whose horns are experimentally lengthened or shortened are respectively more and less likely to win fights. In addition, those whose antlers are removed altogether are treated by their rivals as females. Thus, antler-weapons serve to a great degree as displays whose size opponents appear to correlate with fighting ability.

Rival males pay attention to each other's visual displays when deciding how they will go about the all-important activities of holding resources and inseminating females. The reason is either the display is an accurate indicator of another's ability to defend its resource, or the opponent accepts that it is. 'Honest advertisement' is an important principle in both intra- and intersexual signals. Over evolutionary time, a signal that exaggerates the capabilities of its sender will eventually be ignored by increasingly discriminating receivers. However, a signal that is expensive to build and display, or risky to use, is likely to honestly reflect the capacity of the sender for violence. Paradoxically, displays that 'handicap' the emitter are the most useful in deciding whether it would be prudent to escalate a conflict or withdraw.

Stalk-eyes in flies are a case of what may have been a dishonest display evolving into a handicap and an honest advertisement. Smaller flies typically retreat from face-to-face confrontations with larger opponents and fights are normally between similar sized individuals. Suppose that the size of a rival is assessed by the breadth of the head, as gauged by the degree of overlap between the two sets of eyes. If so, males can appear large and conquer psychologically simply by broadening their faces. As deceitfully widened heads become more common, even further exaggeration is required, and the resulting 'arms race' pulls the eyes farther and farther apart until they are at the ends of extraordinary stalks (in one 8 mm long species from Borneo, the combined length of the stalks is 20 mm). In the process, the stalks have become honest advertisements, genuine burdens that only the most robust males can produce and maneuver. Not only do males use stalk eyes to decide which opponents can be expelled and whether to fight or flee, but females also consider their size when choosing a mate.

The content of intersexual displays

Location cues: long-distance signals. Because males usually benefit more from multiple matings than do females, they typically spend more energy and take greater risks than females to locate mates.

Fig. 1122 The eyes of this male fly (*Achias* sp.) are at the ends of stalks whose combined width exceeds the length of its body. This condition, although usually less extreme, is found in a number of fly families and may be the result of trying to appear as large as possible in the opposing eyes of sexual rivals (drawing by Kevina Vulinec in Sivinski 1997).

When females are scattered through the environment, this often means males travel considerable distances searching for cues to find females. Because it is also in the female's interest to be found by one or more males and proceed with oviposition more quickly than other females, she may emit a relatively inexpensive signal that improves her chances of being located. Sexual pheromones are common female location cues that are typically produced in small, economical amounts and sent out with little risk as few predators or parasitoids specialize in tracking down the emitters of these chemically dilute and sporadic signals.

Modifications of female form or coloration that serve as signals to orient searching males may be less common than pheromones because the distance at which a visual cue can be perceived will generally be less than that of volatile chemicals. In addition, natural enemies without any special sensory adaptations might recognize visual signals as well as, or even better than, conspecific males. However, female location cues do seem to occur. For instance, in certain luminescent beetles like the phengodid *Phengodes nigromaculata*, larviform adult females retain the elaborate system of larval light organs that probably served as an aposematic advertisement of unpalatability. But the adult's lights are much brighter than the larva's and could act as a beacon to searching males whose large, complex male antennae suggest a female pheromone is produced as a longer distance signal as well. An alternative explanation for the brighter lights of adult females may be that chemical signaling requires more time spent exposed on the surface of the ground, and because of their greater vulnerability, females invest more in their aposematic display.

Competition among females to attract males from a distance typically will be less intense than competition among males to attract females. When males produce long-distance signals, whether chemical, acoustic, or visual, it is assumed that the signals are now more expensive than the travels females must undergo to reach the signaler, that the sender may be in greater danger from predators and parasitoids, and that females will be more likely to judge males on the basis of their signals than vice versa and respond selectively to the signals they deem most attractive.

While there are many familiar male long-distance chemical and acoustic signals (e.g., Mediterranean fruit fly, *Ceratitis capitata*, and crickets [Gryllidae]), there seem to be fewer obvious visual examples. Part of the reason may again be the relatively limited range of vision in insects which is better suited to close-up examinations. Even so, there are a number of interesting male visual-location cues. The lights of perched male fireflies (Lampyridae) are visual equivalents of a katydid's (Tettigoniidae) song, and diurnal 'beacons' that appear to advertise male positions occur in certain long-legged flies (Dolichopodidea). Male *Chrysotus pallipes* have much enlarged

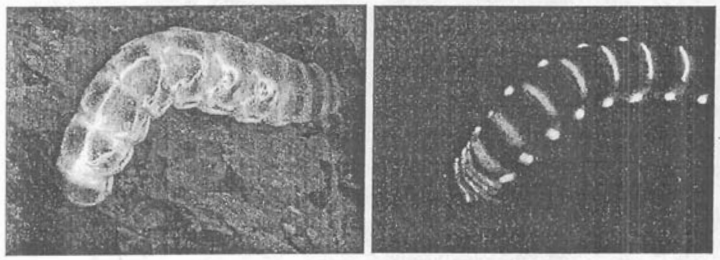

Fig. 1123 A larviform female phengodid beetle (*Phengodes nigromaculata*) (a), and the same insect photographed by its own bioluminescence (b). The relatively bright lights of adult glow-worms may be beacons that help attract mate searching males (photos by J. Sivinski).

and shiny labial palps that emit silver flashes as they signal from the surface of leaves, and the reflected light from the tiny insect is surprisingly bright.

Courtship displays. Courtship implies that the sender of a signal is attempting to overcome resistance in the receiver, and that the display will somehow influence (or manipulate) the receiver to copulate. This element of 'seduction' can occur in long-distance signals as well, particularly those produced by males, and this blurs the distinction between long-distance beacons and courtship performances. However, greater amounts of detailed information, particularly visual information, would be available to insects in close proximity that are aware of each other's presence. Certain sexual behaviors will be unique to such close-up situations and so deserve separate consideration.

The meaning of communications with the opposite sex often is ambiguous, and there are several competing theories that attempt to explain the evolution of courtship displays. These hypotheses can be divided into the following categories: 1) displays promise a material benefit to the receiver, such as a nuptial gift of food or high female fecundity, 2) displays advertise the genetic qualities of the performer through self imposed handicaps, and 3) displays provide neither direct material nor genetic information, but are due to either genetic feed-back ('Fisherian run away selection') or manipulation of the receiver's perceptions ('sensory bias'). It may be that all of these are involved in the evolution of different displays.

Material benefits. The exchange of 'goods' from males to females, i.e., nuptial gifts, have been well documented in several insect groups. Examples include scorpionfly (Mecoptera) males that are required by females to produce captured prey of sufficient size, or else successful sperm transfer is not allowed. Some male Lepidoptera provide large, nutritious spermatophores during mating. The same is true of certain orthopteran males, while other orthopteran and coleopteran males provide nutritious secretions from the mouth or glands.

Such nuptial feeding invites deceit through false appearance. Things can be promised and then withheld to tempt another mate, or be promised but be completely absent. On the other hand, a female attempting to acquire a male's investment might exaggerate her fecundity, and appear to be a bigger mother and better recipient than she really is. When either sex has materials the other requires, be it protein or access to eggs, advertisements, including visual advertisements, they are likely to be elaborated through exaggeration. As in stalk-eyes, the expense of elaboration may eventually become a handicap and forge an honest display.

Empidid or dance flies (Diptera) provide examples of both male and female visual displays evolving in the context of sexual 'commerce.' Predaceous male dance flies often provide mates with a prey item, but sometimes this is wrapped in a silk balloon that might have originally magnified the appearance of the gift and which, in some cases, may no longer hold anything and is perhaps only an empty promise. Even more peculiar are the odd outgrowths of the midlegs of male *Rhamphomyia scurissima*. This mass of swellings suggests the male has a small dead insect in its grasp, and, with this deception, he may be able to lure a gift-seeking female into a sexual encounter.

On the other side of sexual bartering are females whose apparent fecundity influences whether or not they are offered nuptial gifts. In some species, there are sex-role reversals where females swarm and males carrying insect prey choose the largest females to both feed and inseminate. Females may call attention to their abdomens, and the numbers of eggs they contain, with garish, bright silver markings. In several empidid genera, females inflate their abdomens with air until they are nearly spherical, and so may falsely appear to carry extraordinary numbers of eggs.

Genetic benefits. *Drosophila* (Diptera) females that are free to pick their own mates produce more mature offspring over their lifetimes than do females that are provided with randomly chosen males. The implication is that certain males are better sires, and that females are able to recognize their genetic qualities. But what sort of qualities are they choosing and how are they recognized? It may be that phenotypes that have survived to old age or acquired the resources to attain unusually great size are reflections of an underlying genetic capacity to survive and forage effectively. For example, in certain tephritid fruit flies females prefer larger males, although the role of vision in judging size is unknown.

In general, the problem with signals that advertise such characteristics is that they can be exaggerated. Increasingly discriminating females will demand honest advertisements from prospective mates, and

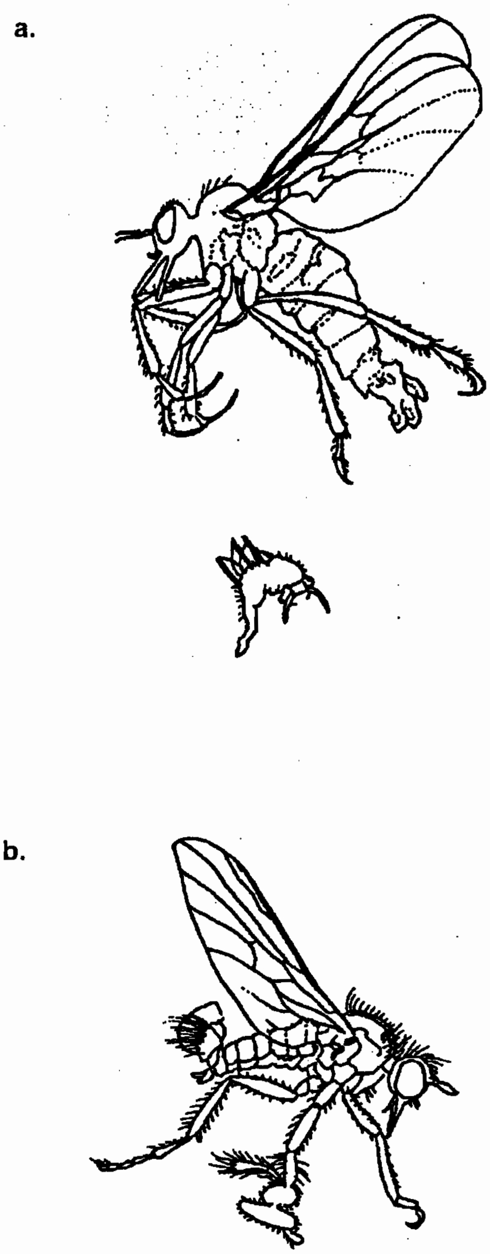

Fig. 1124 Males of many empidid species provide potential mates with an insect cadaver to eat (a). The peculiar outgrowths on the midlegs of the dance fly *Rhamphomyia scaurissima* (b) originally may have mimicked such a nuptial gift and attracted females through dishonest advertisement (drawing by Kevina Vulinec in Sivinski 1997).

signals that are expensive, or dangerous, or otherwise impossible to counterfeit should become preferred. For example, it is hard for a male to appear to be more symmetrical than it actually is. The complexity of embryonic development often results in less than perfect bilateral symmetry, and the greater the number of deleterious recessive alleles in the genotype the more unlikely it becomes. As a result, 'fluctuating asymmetries' in males are windows through which the value of their genes can be perceived and judged. Male *Calopteryx splendens* (Odonata: Calopterygidae) with more homogeneous wing spots perform more displays and obtain more mates, and male cerambycid beetles with more symmetrical antennae are more sexually successful. However, it is not always clear that female insects can visually discriminate fine degrees of asymmetry, and it is possible that they are attracted to male characteristics that co-vary with symmetry. For instance, a male that is more symmetrical may also have the physical capacity to signal for longer periods of time, and it is the signaling duration and not the symmetry that females find attractive.

Expense also insures honesty. A display that requires substantial material to produce, considerable energy to perform, and that places the emitter in danger is likely to be the production of a genuinely fit individual, one that had access to resources and was able to escape predators. Thus, displays are expected to be handicaps that are a burden to the insect outside of its sexual life.

Concentration on sexual matters can make males more vulnerable to predators, and it may be that the riveted attention that males focus on potential mates during courtship is in itself a handicap whose message is that "I possess such strength and agility that I can afford to give you my undivided attention and survive." Other physical trials might reveal genetic quality, e.g., females of the wolf spider *Hygrolycosa rubrofasciata* choose males on the basis of their leg-drumming rates which, in turn, are predictors of their viability.

In addition to risky, arduous or complicated behavior, physical structures may prove both costly to the signaler and attractive to the opposite sex. There are certainly any number of peculiar sexual dimorphisms in insects that could be both displays and handicaps. Many courting insects energetically use their wings, which are also important organs of predator-escape, in displays that might jeopardize their safety. For instance, potentially compromising wing motions are ubiquitous in the courtships of the tephritoid Diptera; e.g., *Callopistromyia annulipes* (Ulidiidae) males 'strut' with wings upraised like a peacock's tail, and rapid wing movements are nearly universal in the sexual interactions of other large taxa like the parasitic Hymenoptera (such motions may also waft pheromones and/or produce acoustic signals).

Colors can attract both the opposite sex and the attention of predators, and in addition, some colors may be difficult or even dangerous to produce. In birds for instance, red pigments are derived from carotenoids that the animal cannot manufacture and must be obtained from food sources. Further, carotenoids are important components of the immune system and their removal from a vital health-function in order to be 'painted' on the body surface may send a powerful message about both the foraging capacities and disease resistance of the signaler. Males often suffer more injuries and greater mortality than females, and this may be due to either more conspicuous colors or more risky mate-searching behaviors that expose them to predators. An illuminating case of dangerous bright coloration, as opposed to dangerous behavior, occurs in *Ischnura* damselflies (Coenagrionidae). Females may be either drably colored or brightly colored like the males ('andromorphs'). Brightly colored females are less likely to be recognized as potential mates and so avoid pestering by males. Because of their male-like appearance, they are able to lay their eggs more efficiently, but, unfortunately, they are also more likely to attract the attention of predators and, in some populations, they have only one-third the life expectancy of their plainer sisters.

Finally, color may indicate the ability of the signaler to avoid or survive debilitating diseases and larger parasites. Females may prefer such males either because they are likely to sire healthy offspring or because healthy males are less likely to transmit a disease during copulation. It has been suggested that the colors and forms of certain dung-feeding male scarab beetles might highlight the mite population they carry and allow females to choose males with lower mite loads.

Fisherian run away selection. If the genes for the expression of a male trait (e.g., an element of a courtship display) and the female preference for the trait are linked, then females that choose the most extraordinary examples of the male characteristic will tend to have daughters with a still more extraordinary 'taste' for the display. The extravagance of the display and the female demand for the extravagant will continue to increase hand-in-hand ("run away" in the sense of positive feedback) until the spiraling expense and danger of the signal are so great that natural selection puts an end to further elaboration. In this process, the display has no 'meaning,' females gain no insights into male genetic or material qualities from the display and choose mates only for their capacity to produce a more or less arbitrarily attractive set of colors, structures and behaviors.

Recently, the popularity of this theory of the origin of displays has suffered somewhat for two reasons. First, phylogenetic studies reveal that male displays have been lost in a number of lineages, much more frequently than previously had been imagined, and this loss is inconsistent with linked traits running away with one another. Second, displays increasingly are found to be reliable indicators of male quality and not simply matters of haphazard fashion. Particularly telling cases of informative signals occur when the same displays that males use to persuade females are also employed in competitive interactions with other males. A sexual rival has no reason to be intimidated by a structure or behavior that is only fashionable and not an advertisement of the ability to acquire a resource or to defend associated females. For example, in the stalk-eyed fly (Diopsidae), *Cyrtodiopsis whitei*, female harems 'roost' in the company of individual males, and females prefer associations with long-stalked males because stalk-eye length is correlated to offspring quality. Eye stalks are also used in antagonistic interactions.

Sensory bias - . 'Sensory bias' theories of the origin of displays suppose that male sexual displays take advantage of preferences that have evolved in females for other reasons, and so manipulate females into responding. This is another type of male signal that tells females nothing useful about male genetic or material qualities, at least in the early stages of its evolution. For example, females of the water mite *Neumania papillator* (Acari: Parasitengona) use vibrations to locate their copepod prey, and males make similar vibrations with their forelegs. Females move toward and clutch vibrating males, and are more likely to do so when they are hungry. It seems favored because they give greater access to the opposite sex. Competition among members of one sex for access to the other results in 'intrasexual selection,' and mate choice and the displays directed to the choosing sex evolve through 'intersexual selection.'

Sexually selected displays presumably resolve competitions and/or facilitate mate choices because receivers evaluate and act on information contained in the display's colors, size and motions. The experimental evidence that arthropods perceive visual displays and then modify their reproductive activities is phylogenetically widespread. Some examples include the sexual response of fireflies (Lampyridae) to patterned electric lights, and female wolf spiders' (Lycosidae) reactions to videotapes of the stylized foreleg movements the males perform during courtship.

The basis of sexually selected signals

Ultimately, both inter–and intrasexual selection occur because of differences in 'parental investment' between the sexes. Parental investment is anything, material or behavioral, that a parent invests in an offspring that increases the offspring's chance of surviving at the cost of the parent being able to invest in other offspring. There is a fundamental sexual dimorphism in parental investment due to the female's initial investment in large, resource rich eggs, and the male's in small, inexpensive sperm. All other things being equal, a female's capacity to reproduce is limited by the resources she can obtain and use to produce her eggs. Multiple mates do not necessarily result in more offspring, although she may be able to choose a mate whose genetic or other qualities, sometimes illuminated through displays, result in her bearing more, or more fit, offspring. On the other hand, ejaculates are cheap and males invest little in the insemination of a female. The more females a male copulates with, the more offspring he will father. As a result, selection favors males that successfully compete with one another for access to mates, often through displays directed both to females and to other males.

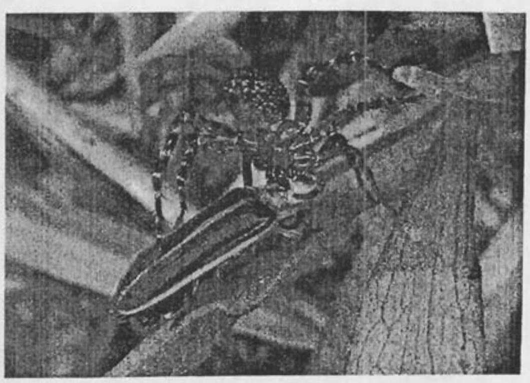

Fig. 1120 There are dangers as a well as opportunities inherent in visual signals. The eye(s) of this spider may have first been caught by the firefly's bioluminescent sexual display (photo by Steven Wing).

There are exceptions to this "grand generality." For example, males of some species of katydids (Tettigonidae) and balloon flies (Empididae) provide females with nutritious 'nuptial gifts,' such as huge protein-rich ejaculates and insect cadavers. As a result, a female's reproduction is influenced by her ability to gain access to gift-bearing males. In these instances there may be sex-role reversals and males choose mates from among competing, displaying females.

Sexual dimorphism and sexually selected displays

In some species, members of one sex differ in appearance from members of the opposite sex. Sexual dimorphism in color is suggestive of a display in one of the sexes. Charles Darwin, for example, was struck by the brilliancy of male butterfly coloration and the relative drabness of females. He, and subsequently others, proposed that sexual selection had generated colors of greater saturation and more precise demarcation in males because they were used in sexual communications while females maintained the ancestral, more cryptic, coloration. Some exceptions to the 'rule' that females bear the more ancestral coloration tend to support the idea that sexual selection has been more important in the evolution of male than female coloration. There are instances in butterflies (Papilionidae), e.g., the African swallowtail, *Papilio dardanus*, where relatively palatable females are 'Batesian mimics' of one or more aposematic-unpalatable species, but males maintain a pattern more typical of closely related species. It seems likely that male-signalers have conserved a coloration that is important in a visual display, and that females, either because they are the display-receiving sex or because they are not involved in intrasexual competitions, were free to abandon their that males have exploited the female's feeding behaviors to increase their rate of sexual contact.

Manipulative visual displays occur in the wolf spider (Lycosidae) genus *Schizocosa*. Males perform leg-waving courtships, but the various species have different degrees of foreleg ornamentation. Female spiders will orient toward video tapes of male courtships, and prefer the images of males with tufts of hair on their legs, regardless of whether or not their conspecific males have such hair-tufts. Thus, females in both tufted and untufted species appear to have a pre-existing preference for hairy legs that males of some species take advantage of and that males of other species do not.

This taste for leg-tufts might be a byproduct of hunting behaviors where female spiders must orient toward and approach small moving objects in their environment. Because such a response is necessary for the display-receiver to obtain food, it is difficult for her to completely ignore the signaler, but females might become more discriminating over time and sensory bias signals could evolve to carry information about male quality. For example, female *Schizocosa* spp. are more responsive to males with symmetrical forelegs, and such symmetry may be the result of developmental stability or a successful fighting career. Foreleg displays that now are showcases for symmetry may be elaborations of what began as lures.

Copulatory and postcopulatory displays

A female insect may choose the sire of her offspring at several points prior to oviposition. Her responses to precopulatory courtships determine whether or not she will mate. But even while coupled, she may choose to direct sperm to different portions of her reproductive tract where they will either be used for fertilizations, or be shunted away into places where they will languish or perish. Following mating she may simply eject sperm from a particular male, or copulate again with a more suitable male whose new ejaculate will block the old sperm from reaching the ova.

Because of these opportunities for 'cryptic female choice,' males may guard mates or continue courting mates with displays during and even after insemination. There are a number of male copulatory behaviors that might qualify as visual appeals to females making cryptic choices. *Sabathes cyaneus* is an unusually brightly colored mosquito whose mid legs end in a feathery 'paddle' of elongate iridescent blue and gold scales. Males fly toward resting females with their paddles extended, land nearby, suspend themselves by their forelegs, and then swing and wave their ornaments. 'Waggling,' during which the midlegs continue to rise and fall, continues through the copulation. Mounted males of the long-legged fly *Scapius platypterus* (Dolichopodidae) insure their visual signals will be observed by resting their front legs over the female's head while the midlegs are held to the side near her eyes and waved back and forth. Males of the micropezid fly *Cardiacephala myrmex* close the gap between their foreleg motions and their mates by alternatively scratching and regurgitating on her eyes. Not only flies apply their ornaments to female eyes during copulation. Male wasps in the genus *Crabo* (Hymenoptera: Sphecidae) have the front tarsi dilated into horny plates punctured by membranous dots giving them a sieve-like appearance. During mating, these are placed over the female eyes, perhaps resulting in a specialized visual signal similar to what would be obtained by shining a light through an antique computer 'punch card.'

Mating systems and visual displays

Arthropods seek mates in a number of ways and in a variety of places, some suited to the production of visual displays and others not. Swarms, where multiple males (or rarely females) fly in place, sometimes by the thousands, over a spot or 'marker' are both common and seemingly poor places to advertise to potential mates. With numerous insects swooping about each other, signals, particularly pheromones, would be difficult to track back to their emitter. And, if the emitter cannot be identified, then cheaters who do not invest in a signal but fly about in another's 'perfume-cloud,' have an energetic advantage that would eventually lead to their increase and then to the collapse of the entire display system. Visual displays are somewhat more likely, but still suffer from a poor capacity for individual recognition. For example, swarming mosquitoes are typically drab, but non-swarming species are often colorful. However, if flight is slow enough and swarmers separate enough, then visual signals can and do evolve. Small species of Mayflies (Ephemeroptera) sometimes have glassy wings and their swarms resemble falling snowflakes in the sunshine. Some of the most

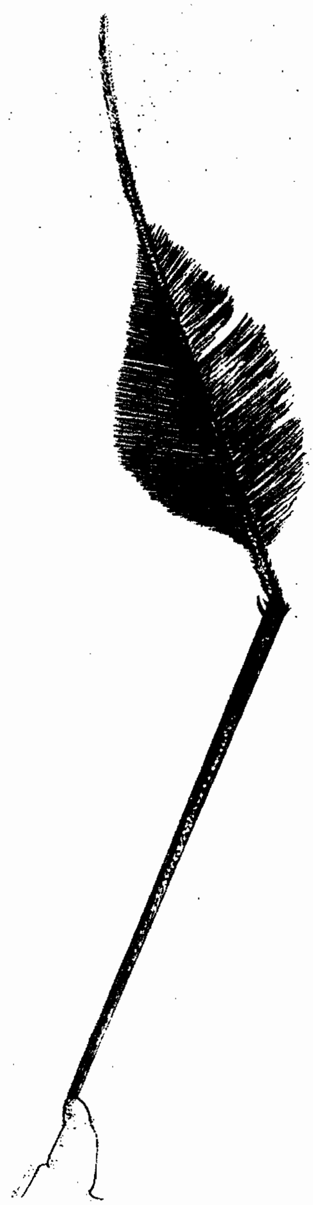

Fig. 1125 Mosquitoes are rarely ornamented. An exception are males of the genus *Sabathes* whose midlegs are decorated with iridescent 'feathers.' This feather is waved before females both prior to and during mating (drawing by Kevina Vulinec in Sivinski 1997).

remarkable insect ornaments occur in certain swarming, flat-footed flies (Platypezidae). Species of the North American genus *Calotarsa* have enlarged hindlegs that bear a curious collection of projections and glittering aluminum-colored flags. They fly in a slow and dignified manner while allowing their "...hind feet to hang heavily downward and look as if they were carrying some heavy burden."

Aerial displays by non-swarming insects are easier to evolve and maintain because the complications of confusing neighbors are diminished. The brighter colors, and occasionally unique markings, of male butterflies are displayed in intrasexual encounters and some of these occur during aerial conflicts. In many species of *Photinus* fireflies (Lampyridae), males make nocturnal flights, advertising their availability with flash patterns. These patterns of flashes elicit response flashes from perched females, and through flash dialogues males locate females, land near them, and mating occurs. Some species of *Photuris*, another genus of fireflies, are aerial predators of signaling *Photinus* males. The flashing signal is more difficult for the predator to track in flight than a continuous glow. Flashing may have evolved from an ancestral continuous glow in response to this predation pressure.

Once courtship occurs on the ground or leaf surfaces or some other platform, there is finally a stable stage on which males can easily perform elaborate behaviors with complexly patterned ornaments and be relatively easily recognized as individuals with their own particular messages to send. Ground-based mating systems can consist of single males searching or occupying a signaling site (often a resource) or groups of males either aggregated at a resource or gathering in non-resource based 'leks.' Visual displays occur in these different mating systems. Many of the highly decorated male dolichopodid flies appear to be solitary, or at least not tightly aggregated. Striking sexual dimorphisms are also encountered in lekking species in other families. An unusual example of the latter is the scuttle fly, *Megaselia aurea* (Phoridae). Like most phorids, males are nondescript flies, cream and grey in color, but females are yellowish orange with an iridescent orange patch on their dorsal surface. In addition to their unusual coloration, females have the peculiar habit (for their sex) of gathering on leaf surfaces in groups of up to a dozen or so. Males visit these sex-role reversed leks, pair with a female, and fly off to copulate on nearby vegetation. The bright orange of the lekking females suggests a visual display directed either to female lek-mates or male visitors.

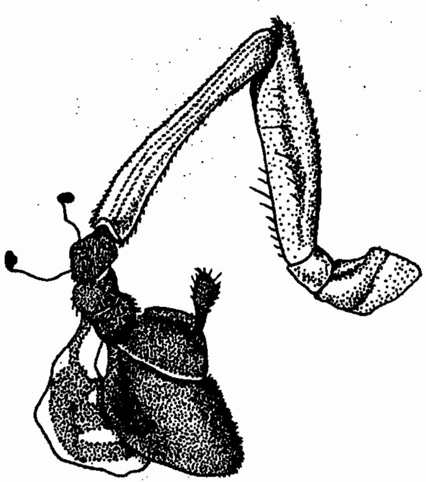

Fig. 1126 Swarming insects are seldom in a position to emit visual signals. The intertwining flights of numerous insects are simply too confusing. However, there are exceptions and the hindlegs of the swarming flatfooted fly *Calotarsa insignis* are a spectacular example of insect ornamentation (drawing by Kevina Vulinec in Sivinski 1997).

The locations of ornaments and colors

The structures and colors used in visual displays occur all along the arthropod body, but there are certain points of concentration. Some display locations emphasize a particular body part. Female dance flies that call attention to, or exaggerate, the size of their ovaries enlarge and color their abdomens, and ornaments used in male-male interactions are often on the head, perhaps because the head is used in the pushing style of combat typical of Diptera. Elaborations such as eyes elongated into cow-like horns (*Zygotricha dispar* [Drosophilidae]) and antlers and eye-stalks may be embellishments of actual weapons that now also advertise sexual competitiveness.

Movement can be an important component of a signal either because receivers are likely to notice the motion and so be more likely to see the ornament, or because the motion itself is the message and the movement is made more obvious by the ornament. In either case, ornaments or motions could serve as 'amplifiers' that attract the attentions of the opposite sex to the display. It has been argued that a simple preference for the first male a receptive female might see could select for such amplifiers, and that competitions among amplified males to be the first noticed might act as 'mate-filters.' On average, females would be most likely to couple with active, easily seen males whose apparency is a correlate of a good genetic constitution.

This premium on movement has served to concentrate signaling onto moveable body parts such as legs, wings, labial palps, antennae, and even the external genitalia. In dolichopodid flies, the male genital region is sometimes much enlarged (the hypopygium) and this may be raised and lowered during the male's courtship advance (e.g., *Dolichopus omnivagus*). In one unidentified species, males rise up on their long legs, beat their wings, lower the hypopygium until it hangs perpendicular to the body, and then slowly twirl their genitals. Dipteran legs are adorned with signaling devices that range from simple flags of enlarged setae to bizarre banners of hairy projections and strange devices. In yet another dolichopodid, *Campsicnemus magius*, the front legs are so swollen, pendanted and hairy that critics suggested the original specimens were deformed by fungi. Likewise, the fore tibia of the flower fly (Syrphidae), *Tityusia regulas*, are "enormously thickened, grooved, twisted and distorted" with an "extremely long, extremely matted" dark pile of fringe, and tarsi are extravagantly flattened with the lateral edges of the second, third, and fourth segments prolonged into narrow, down-curving lobes. Other examples occur outside of the Diptera, e.g., some male leaf-footed bugs (Coreidae) may use colorful expansions of both hind leg and antennae in defense of territories such as flower heads.

As noted earlier, while color can appeal to the opposite sex or deter rivals, it may also attract predators, and displays that can be produced only when the appropriate receiver is in a position to appreciate the signal may be safer than those that are on all the time. Ornaments on some moveable structures have the advantage of concealing and then revealing a signal in all its splendor. Consider any number of butterflies (e.g., the white M hairstreak, *Parrhasius m-album* [Lycaenidae] or the Florida purplewing, *Eunica tatila* [Nymphalidae]) whose outer wing coloration is dull and cryptic, but whose inner surface is dazzlingly bright. Such an insect at rest is difficult to detect, but with its wings opened while on its perch or in flight, it is an iridescent beacon (although one must consider the habitat, as periodic flashes of iridescence in the dappled light of a forest may be misleading or disguising).

The phyletic distribution of visual sexual displays

Different arthropods have different capacities and opportunities for the production of visual sexual displays. Diurnal butterflies have a greater chance to employ visual signals than do nocturnal moths. As noted earlier, jumping spider (Salticidae) vision lends itself to the reception of color and complex movement, while the eyes of the related wolf spiders (Lycosidae) do not. The frenetic mass flights of small swarming flies are incompatible with visual signals, while the largely surface-bound foraging habits of dolichopodid flies may give them a ready stage on which to perform elaborate displays and so be the reason they are among the most ornamented Diptera.

As a result of these and other differences, there appears to be a clumped distribution of visual displays. There is hardly enough research to quantify this distribution, but it seems that the more derived flies (Brachycera) have a disproportionate number of apparent visual displays. Butterflies, luminous beetles and Odonata are other obvious hotspots of visual communication.

Conclusion

The diversity of arthropod visual signals is immense, owing to the evolutionary plasticity of the arthropod body and the behaviors used in combination with visual signals to modify and enhance their effects. Visual signals are adapted to a wide variety of habitats and contexts. As noted above, not all arthropod signaling evolved by sexual selection, as not all colorful arthropods are signaling to sexual partners or rivals. In fact, given the limitations of insect eyes, colors and patterns more often than not may be directed to visually acute predators such as birds and serve to startle, warn of unpalatability, or to mislead.

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VITAMINS. Vitamins are nutrients needed for normal growth of insects. Those required are thiamine, riboflavin, pyridoxine, niacinamide, pathothenic acid, biotin, folic acid and choline. Some insects also require carnitine, ascorbic acid, carotene, vitamin B-12, vitamin E, and others.

VITELLINE MEMBRANE. A membrane surrounding the egg, which in turn is surrounded and protected by the chorion.

VITELLOGENESIS. The formation of yolk in the developing egg.

See also, OOGENESIS, ENDOCRINE REGULATION OF REPRODUCTION, REPRODUCTION.

VITELLOGENIN. The major yolk proteins are called vitellogenins while being transported to the hemolymph, and consist of large glycolipoproteins which are produced by the fat body and secreted for uptake by maturing oocytes. Not all yolk proteins are vitellogenins, however, and in higher Diptera the yolk proteins are small polypeptides. See also, ENDOCRINE REGULATION OF REPRODUCTION

VIVIPAROUS. Organisms that bear living young, as opposed to eggs.

VOLATILITY. Ability of a substance to evaporate or vaporize.

VOLUNTEER PLANTS. The unexpected and undesired emergence of plants, usually self-seeded by the previous plants.

VULVA. The opening of the vagina.